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A MORPHOLOGICAL STUDY OF BOTHRIOCEPHALID CESTODES FROM FISHES *

A. R. Cooper

In this study of North American cestodes of the order Pseudophyllidea the writer has used Lühe's (1902) revision rather than his later (1910) classification, since the family Caryophyllaeidae has not been considered. The order is represented in both marine and freshwater hosts by a number of more or less isolated genera and species, three of the latter of which are new. It has been found necessary to expand the family Diphyllobothriidae Lühe and to erect two new subfamilies, Haplobothriinae and Marsipometrinae, to accommodate the genera Haplobothrium Cooper and Marsipometra gen. nov., respectively.

DIPHYLLOBOTHRIIDAE

The separation of this family from the Ptychobothriidae Lühe only on the basis of the presence or absence of a permanent sac-like enlargement of the uterus (the uterus-sac) and opercula on the eggs would probably now be considered as invalid, were there not other and perhaps more important characters for their differentiation. This is due to the presence of a uterus-sac in the genus Haplobothrium, as has already been emphasized by the writer (1914), and the form of the eggs in Marsipometra.

The only two genera of the subfamily Ligulinae Lühe, namely, Ligula Bloch and Schistocephalus Creplin, are present, each with the single species only that has been accepted by the European workers, particularly Lühe (1910). Both *L. intestinalis* Linnaeus and *Sch. solidus* (O. F. Mueller) are found in the advanced larval condition in the body-cavities of several small teleostean fishes, while the adults live in the intestines of piscivorous birds. Owing to the fact that there are several discrepancies among the existing descriptions of both of these forms, I found it necessary to make a detailed study of their morphology with the view to clearing up the situation.

As already pointed out (Cooper, 1914), the genus Haplobothrium occupies a unique position in the family. What was formerly considered to be the scolex (Fig. 3) is now known to be merely the foremost segment of the secondary strobila. The true scolex (Figs. 1 and 2) is cylindrical or club-shaped and, unlike any other Bothrio-

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cephalid yet described, has as organs of attachment four eversible proboscides instead of two simple or modified bothria. It thus bears a remarkable resemblance to the scolex of the members of the order Trypanorhyncha, which is emphasized by the fact that each proboscis consists of an eversible portion, a muscular bulb for its activation, and a permanently protruded stump, quite comparable morphologically as well as physiologically with the three divisions of the trypanorhynchid proboscis. The manner of segmentation in this species is also peculiar. As shown in Figure 1, the larva or plerocercoid forms at its posterior end segments which by growth and subdivision in their anterior regions only become, after separation from the primary chain, the secondary strobilas already described (Cooper, 1914a). The genital organs resemble those of the subfamily Diphyllobothriinae Lühe in that they are simple in each proglottis while the openings are all surficial,* ventral and median. The vitelline follicles, as well as the testes, are situated, however, in the medullary parenchyma and within the nerve strands. Other characters which are important in the separation of this (Haplobothriinae) from the other subfamilies are the armament of the cirrus with minute spines and the division of the uterus into a much coiled proximal uterine duct and a large uterus-sac.

As has already been emphasized in the generic diagnosis (Cooper, 1914: 1-2) the nervous system consists of two chief strands situated in the medullary parenchyma outside of the vitelline follicles, uniting in the anterior end of the secondary strobila to form a nerve-ring, and eight collateral strands, four around each main tract, the latter in the jointed portion of the strobila only. In the true scolex, on the other hand, these main tracts are connected by an irregular transverse commissure (Fig. 4), situated among the proboscides, from which branches pass not only to the bulbs, but to the large ganglionic mass (Figs. 2 and 5) behind them. Four large tracts from the latter pass into the bases of the bulbs for the innervation of the retractor muscles of the eversible portions of the proboscides. In the secondary scolex the single large median and two smaller lateral excretory vessels all unite behind the nerve-ring to form a vesicle, but in the primary scolex they are connected not only by numerous large branches among the proboscis-bulbs, but by a single large median frontal loop.

The subfamily Cyathocephalinae Lühe is represented by both genera, Cyathocephalus Kessler and Bothrimonus Duvernoy. The species of the former, found only in *Coregonus clupeiformis* (Mitchill), the common whitefish, resembles the European *C. truncatus* (Pallas) in several points, but in others it is so radically different that it has been considered as new and given the name *Cyathocephalus americanus* sp. nov. The chief nerve strands are connected anteriorly by a number of fine nerve commissures instead of a single one. The opening of the vagina is behind that of the uterus, while none of the genital apertures is surrounded by papillae or sphincter muscles. There is no enlargement of the vas deferens just before entering the cirrus-sac nor connective tissue sac surrounding the whole of the coiled duct as in *C. truncatus*. Furthermore, while the cirrus-sac is not provided with special dorsal retractor muscles, it is surrounded dorsally and laterally by a large mass of peculiar glandular pigmented cells (Fig. 9) the function of which has not yet been determined. The absence of a "connective tissue and muscular sac" surrounding the beginning of the vagina and any such "shell-gland" as described for the European form are also of great importance from a morphological as well as a systematic standpoint.

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* The word "surficial" has reference to the dorsal and ventral surfaces of the strobila.

The generic name Bothrimonus Duvernoy has been taken to include both Bothrimonus and Diplocotyle Krabbe, as contended by Schneider (1902). Of this genus there is present only one species, *B. intermedius* sp. nov., which, while resembling *B. nylandicus* Schneider (1902) in particular, differs from it rather in an aggregate of details than in a limited number of special diagnostic value. The nervous system is, however, radically different in that just behind the scolex each chief strand divides into two sagittally directed branches which are united frontally by a diffuse and not compact commissure.

I have given the name Marsipometra gen. nov. to *Dibothrium hastatum,* briefly described by Linton in 1897, owing to the fact that it cannot be accommodated in any of the existing genera, altho it has several features in common with some of those belonging to the subfamily Triaenophorinae Lühe. The sagittate scolex (Fig. 10), the proglottides, and the segmentation itself are all quite distinct and regular in their nature. Nor is this confined to the external features, for the arrangement of the internal organ-systems is also peculiarly diagrammatic (Fig. 11). The opening of the cirrus and vagina at the bottom of a comparatively capacious genital cloaca (Fig. 13) is marginal and irregularly alternating, while the uterine aperture is surficial, ventral, and on the same level with the genital atrium or very slightly behind it. A conspicuous hermaphroditic duct and a cloacal sphincter are also present. The testes are situated in the medulla between the nerve strands, which are far towards the margins and dorsal to the cirrus-sac and vagina, and are arranged in two lateral fields united ahead of and behind the uterus-sac and central genital ducts. There is no vesicula seminalis immediately proximal to the cirrus-sac, but the receptaculum seminis is comparatively large, rather long, and sharply separated from the continuation of the vagina, the spermiduct. The ovary is comparable to that of some of the members of the Triaenophorinae in that it is not exactly in the median line, but slightly approaching the margin bearing the genital cloaca. It is also reniform, with tubulolobular wings and a thick, ventrally situated isthmus (Fig. 11). The shell-gland, ahead of the ovary, is likewise not exactly in the median line, but towards the genital cloaca. The vitelline follicles, as shown in Figure 11, are arranged among the body muscles, not in two lateral fields, but continuous from side to side in the anterior and posterior regions of the proglottis. Like the testes they are not continuous from proglottis to proglottis. The uterus-sac is pouched (whence the generic name) and occupies the whole of the medulla dorsoventrally, but not transversely in gravid joints. As in the genus Bothriocephalus, it is developed by the enlargement inwardly of that portion of the duct passing thru the cortical parenchyma. The uterus-opening is towards the margin bearing the genital cloaca, especially in the younger segments; in gravid proglottides it is naturally more median, but never exactly in the median line. Perhaps the most outstanding feature of *Marsipometra hastata* is the fact that the eggs are not provided with opercula, in which particular it is isolated from all other members of the family Diphyllobothriidae. Finally, as regards its systematic position, my study of the anatomy of this species leads me to conclude that not only must it be accommodated in a few genus, but also in a new subfamily the name for which will then be Marsipometrinae subfam. nov.

In the material studied the subfamily Triaenophorinae Lühe was represented by Triaenophorus Rudolphi and Fistulicola Lühe. Altho all of the specimens of the former were larval, two forms from several host species were recognized as being probably the same as the European *T. nodulosus* (Pallas) and *T. robustus* Olsson. Fistulicola is, on the other hand, represented by the single species *F. plicatus* (Rud.) from *Xiphias gladius* L., the swordfish.

PTYCHOBOTHRIIDAE

Lühe's use of the distinction between the two main divisions of the uterus, the uterine duct and the uterus-sac or uterus proper, in the separation of this family from the Diphyllobothriidae, is justified by my study of the developmental relationships of these parts with each other in both Bothricephalus s.str. Lühe and Clestobothrium Lühe. In the species of these two genera the common rudiment of the uterus separates into its two constituents soon after it is formed, which has also been shown (Cooper, 1914 and 1914a) to obtain in the case of *Haplobothrium globuliforme*. Furthermore, in most of the species of the former genera there is to be seen a method of segmentation of the strobila, which, so far as I am aware, has not yet been described. It consists of a gradual and more or less regular subdivision of a primary segment, which arises from the base of the scolex, into secondary, tertiary, and quaternary subsegments, and even those of the fifth and sixth orders; or into two, four, eight, sixteen, and thirty-two (or more), respectively. Usually, however, the formation of these subsegments does not proceed with the same degree of regularity in all parts of the primary segment, as shown in Figure 18, where the sizes of the dots at the side indicate the values of the subdivisions; there is a sort of dominance of the anterior over the posterior region. This also applies, as can be seen, to the major segments as well, and is on the whole quite comparable to the dominance observed in the experimental regeneration of portions of various planarian worms.

Both of the two well known European species of Bothriocephalus, namely, *B. scorpii* (O. F. Mueller) (=*B. punctatus* Rud., =*B. bipunctatus* Lühe) and *B. claviceps* (Goeze) are recognized and accepted by the writer as American species also, while *Dibothrium manubriforme* Linton and *D. occidentale* Linton are redescribed and placed in the genus Bothriocephalus. *D. laciniatum* Linton and *Bothriocephalus histiophori* Shipley are deleted owing to the fact that they are both considered to be identical with *B. manubriforme.* On the other hand, a fresh-water form, found chiefly in *Stizostedion vitreum* (Mitchill), the wall-eyed pike, is described as new under the name of *Bothriocephalus cuspidatus* sp. nov. It is a medium-sized cestode, up to 180 mm. in length by 2.75 mm. in breadth. The comparatively large scolex (Figs. 14 and 15) is provided with a very prominent terminal disc, deeply notched surficially, and long narrow bothria, quite deep posteriorly. The first segments, while subcuneate in outline and with prominent posterior borders, are almost circular in transection; the middle gradually broaden until they become much broader than long: and the posterior are two to four and a half times wider than long. The genital cloaca is deep and funnel-shaped, and into it the vagina opens close behind the cirrus, the hermaphroditic duct being obscure. The testes on each side of the median genital complex are separated into two unequal fields by the nerve strand (Fig. 16). The cirrus-sac (Fig. 17) is quite large and prominent, being as much as 0.25 mm. in length (depth) and 0.20 mm. in diameter; as shown in Figure 16, it is not exactly median in position. While the ovary is a rather compact organ, the vitelline follicles occupy almost the whole of the cortex, are very numerous (800 to 1000 per proglottis), and are strongly united dorsally and ventrally as well as laterally. The uterine duct is confined to one side of the median line and constantly opposes the cirrus-sac or coils of the vas deferens, depending on the degree of maturity of the genitalia, both alternating irregularly from side to side. The spherical uterus-sac, on the other hand, occupies when gravid one-third of the transverse diameter of the segment and has its opening in the median line very close to the anterior edge of the latter.

Clestobothrium crassiceps (Rud.), the type and only species of the genus, occurs only in *Merluccius bilinearis* (Mitchill), the silver hake or whiting of the Atlantic coast. Its anatomy has been thoroughly studied by the writer and the somewhat meager descriptions in the European literature greatly augmented, some errors being at the same time corrected.

The other subfamily of this family, the Amphicotylinae Lühe, is represented by the genus Abothrium van Beneden only. Of this genus only *A. rugosum* (Batsch) and *A. crassum* (Bloch) are found in general in marine Gadidae and Salmonidae, respectively. Specimens from *Lota maculosa* LeSueur were considered to belong to the latter species, altho in Europe Lota has been said to harbor the former (vide Lühe, 1910). As a matter of fact, *A. rugosum* presents not a few difficulties as regards its specific identity in Lota in particular, which was keenly felt by the writer in the absence of European material for comparison.

Apart from the species dealt with here the following have also been reported from fishes in America: *Dibothrium* (*Anchistrocephalus*) *microcephalus* (Rud.), *D. aleuterae* Linton, *D. tortum* Linton, *D. cynoscioni* [Linton] Ariola, *D. cordiceps* Leidy, and *D. speciosus* Leidy; but since adult material of none of these was available for study, they must remain for the time being at least as *species inquirendae*. The same may also be said in a certain sense of *Bothrimonus sturionis* Duvernoy 1842, which needs to be reinvestigated from the standpoint of the differentiation of the species of and of the genera Bothrimonus and Diplocotyle (vide supra).

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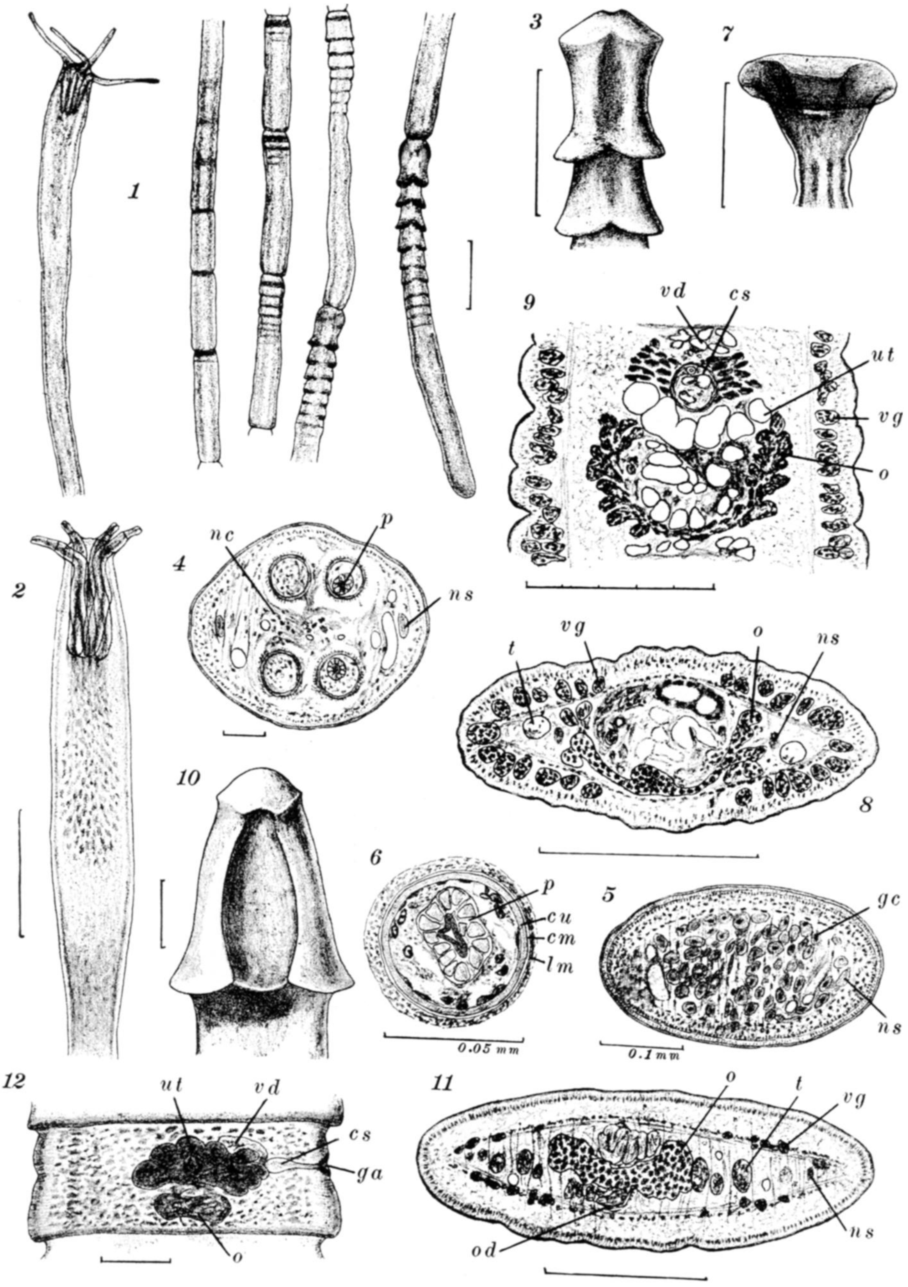
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PLATE 1

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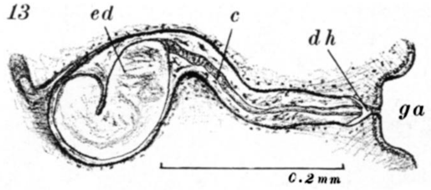

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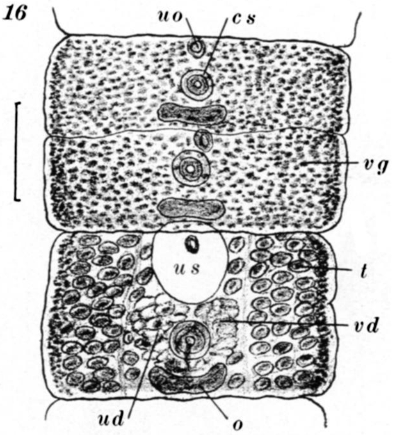

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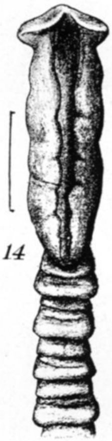

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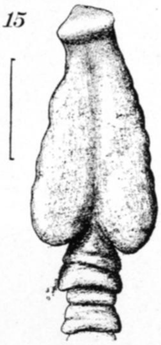

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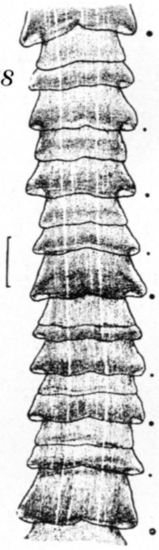

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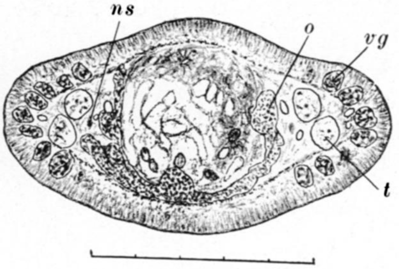

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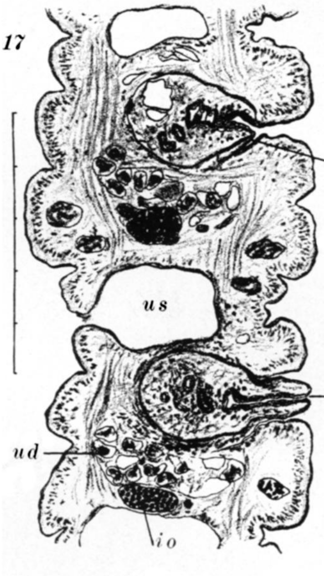

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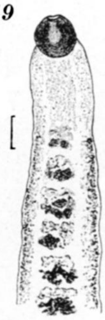

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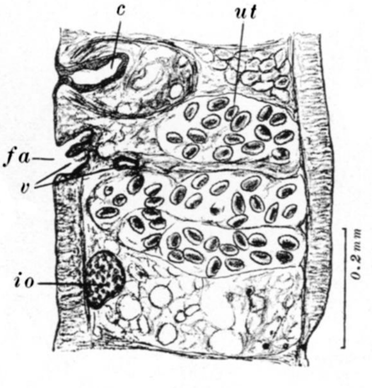

PLATE II

EXPLANATION OF FIGURES

All drawings were made with the aid of the camera lucida. Unless otherwise labeled, the lines indicating the magnifications are 0.5 mm. in length.

c	cirrus
cm	circular muscles
cs	cirrus-sac
cu	cuticula
dh	hermaphroditic duct
ed	ejaculatory duct
fa	female atrium
ga	genital atrium
gc	ganglion cells
io	isthmus of ovary
lm	longitudinal muscles
nc	nerve commissure
ns	nerve strand
o	ovary
od	oviduct
p	proboscis
t	testis
ud	uterine duct
uo	uterus opening
us	uterus-sac
ut	uterus
v	vagina
ud	vas deferens
vg	vitelline glands

PLATE I.

Fig. 1.—*Haplobothrium globuliforme,* primary strobila, showing formation of secondary strobilas, toto preparation.

Fig. 2.—*Haplobothrium globuliforme,* scolex, toto.

Fig. 3.—*Haplobothrium globuliforme,* secondary scolex, surficial view.

Fig. 4.—*Haplobothrium globuliforme,* transection through scolex.

Fig. 5.—*Haplobothrium globuliforme,* transection through the ganglionic mass.

Fig. 6.—*Haplobothrium globuliforme,* transection through single proboscis bulb.

Fig. 7.—*Cyathocephalus americanus,* scolex, toto.

Fig. 8.—*Cyathocephalus americanus,* transection through ovarian isthmus.

Fig. 9.—*Cyathocephalus americanus,* frontal section of ripe proglottis.

Fig. 10.—*Marsipometra hastata,* scolex, surficial view.

Fig. 11.—*Marsipometra hastata,* transection through ovarian isthmus.

Fig. 12.—*Marsipometra hastata,* toto of ripe proglottis.

PLATE II

Fig. 13.—*Marsipometra hastata,* cirrus-sac from a transection.

Fig. 14.—*Bothriocephalus cuspidatus,* scolex, surficial view.

Fig. 15.—*Bothriocephalus cupidatus,* same, lateral view.

Fig. 16.—*Bothriocephalus cuspidatus,* toto of ripe proglottides, posterior in deeper optical section.

Fig. 17.—*Bothriocephalus cuspidatus,* median sagittal section, composite.

Fig. 18.—*Bothriocephalus manubriformis,* an anterior primary segment; the sizes of the dots at the side indicate the values of the subdivisions.

Fig. 19.—*Bothrimonus intermedius,* toto of anterior end, showing genitalia.

Fig. 20.—*Bothrimonus intermedius,* transection through ovarian isthmus.

Fig. 21.—*Bothrimonus intermedius,* median sagittal section.